RFLP Maps Based on a Common Set of Clones Reveal Modes of Chromosomal Evolution in Potato and Tomato

Merideth W. Bonierbale, Robert L. Plaisted and Steven D. Tanksley

Department of Plant Breeding and Biometry, Cornell University, Ithaca, New York 14853

Manuscript received July 26, 1988
Accepted August 29, 1988

ABSTRACT

Potato (*Solanum tuberosum* L.) and tomato (*Lycopersicon esculentum*) are members of the Solanaceae (nightshade family) and have the same basic chromosome number ($x = 12$). However, they cannot be cross-hybridized and, until now, it was unknown how conserved the gene order might be between these two species. We report herein the construction of a genetic linkage map of potato chromosomes based on genomic and cDNA clones from tomato. The potato map was drawn from segregation data derived from the interspecific cross *S. phureja* × (*S. tuberosum* × *S. chacoense*) ($2n = 2x = 24$), and consists of 135 markers defining 12 distinct linkage groups. Nearly all of the tomato probes tested hybridized to potato DNA, and in most cases, the copy number of the employed clones was the same in both species. Furthermore, all clones mapped to the same linkage group in both species. For nine chromosomes, the order of loci appears to be identical in the two species, while for the other three, intrachromosomal rearrangements are apparent, all of which appear to be paracentric inversions with one breakpoint at or near the centromere. These results are consistent with cytogenetic theory, previously untested in plants, which predicts that paracentric inversions will have the least negative effect on fitness and thus be the most likely form of chromosomal rearrangements to survive through evolutionary time. Linkage maps based on a common set of restriction fragment length polymorphism markers provide a basis for uniting the previously separate disciplines of tomato and potato genetics. Using these maps, it may now be possible to test theories about homologies or orthologies of other genes, including those coding for disease resistance and stress tolerances.

THE potato (*Solanum tuberosum* L.) is the most important food crop of the plant family Solanaceae, which contains some 3000 species including tomato (*Lycopersicon esculentum* Mill.), tobacco (*Nicotiana tabacum* L.), petunia (*Petunia hybrida* Hort. Vilm.-Andr.), eggplant (*Solanum melongena* L.), and garden pepper (*Capsicum annuum* L). The tuber-bearing Solanum are one relatively small group of a very large genus and include approximately 170 species. The basic chromosome number of potato, like most other solanaceous species, is $x = 12$ and wild forms range from diploids to hexaploids.

Tomato and potato are members of the same tribe (Solanaceae) (D'ARCY 1976), have nearly identical karyotypes and contain comparable monoploid amounts of nuclear DNA (0.7 pg). The fact that the two species cannot be cross-hybridized has prevented detailed comparative genetic studies and, by-in-large, genetics of the two species have remained distinct and nonoverlapping. In addition, the heterozygous (outbreeding), tetraploid nature of the cultivated potato, and lack of useful genetic markers, has hindered the construction of a genetic linkage map for this species.

The objectives of the research reported here were: (1) to construct a linkage map of potato based on restriction fragment length polymorphism (RFLP) markers, and (2) to determine the degree of similarity between potato and tomato chromosomes with respect to gene order. Genetically, tomato is one of the best-characterized plant species with well-populated linkage maps based on both morphological and molecular markers (TANKSLEY, MUTSCHLER and RICK 1987). By using previously mapped clones isolated from the tomato, we have been able to accomplish both of the stated goals. The construction of comparative maps based on a common set of clones provides a basis for uniting tomato and potato genetics, an accomplishment mutually advantageous for research in both species.

MATERIALS AND METHODS

Plant materials for segregation analysis: Parents and tuber progeny of an interspecific, diploid Solanum cross were obtained from C. QUIROS and D. DOUCHES, University of California, Davis. The pistillate parent of the cross (84S10) was an accession of the diploid species *Solanum phureja* Juz. et Buk. The staminate parent (T704) was an interspecific clone obtained by the hybridization of a dihaploid *Solanum tuberosum* ($2n = 2x = 24$) and a member of the diploid species *Solanum chacoense* Bitt. Attractive features of this population were its diploid constitution, prior characterization of isozyme loci (DOUCHES and QUIROS 1987), and the high likelihood that it would exhibit polymorphism at the DNA level. The mapping population consisted of 65 F_1

progeny, among which segregation of alleles from the interspecific parent was monitored for genetic mapping. Plants were propagated clonally in the greenhouse at Cornell University. The *S. phureja* clone and the *S. tuberosum* × *S. chacoense* hybrid will be referred to hereafter as *phu* and *tbr-chc*, respectively (HUAMAN and ROSS 1985).

DNA isolation, restriction digests, electrophoresis and blotting: Isolation of potato genomic DNA from leaf tissue was as described for tomato (BERNATZKY and TANKSLEY 1986a), except that sodium bisulfite was used instead of mercaptoethanol. Digestions with the following endonucleases (BRL) were performed according to the manufacturer's instructions using 2 units of enzyme per μg of DNA: *Eco*RI, *Eco*RV, *Hin*dIII, *Dra*I, *Xba*I, *Bst*NI, *Hae*III, *Taq*I, *Mbo*I, *Msp*I and *Hin*fI. Seven micrograms of digested potato DNA were loaded and separated on 0.9% agarose gels. Electrophoresis and Southern blotting were conducted as described by BERNATZKY and TANKSLEY (1986a). The only modifications of the above-mentioned protocols were the substitution of Genescreen plus (NEN) filters for Zetabind, and the use of capillary blots instead of dry blotting. On survey filters, the parents were represented in each of 11 pairs of restriction digests. Four to six replicated progeny filters, including one lane of digested tomato DNA (*L. esculentum* cv. VF36), 65 potato progeny, and one lane of each of the potato parental DNAs, were prepared from bulk digests with each enzyme.

DNA probes, labeling and hybridization: Both cDNA and genomic clones were used as probes for mapping the potato genome.

Construction of the cDNA and size-selected (0.5–3.0 kb) *Pst*I or *Eco*RI genomic libraries from tomato have been described elsewhere (BERNATZKY and TANKSLEY 1986a; TANKSLEY *et al.* 1987). The loci detected by hybridization of cDNA clones were designated *CD1*, *CD2*, etc., and those detected by the genomic clones are designated *TG1*, *TG2*, etc. Duplicate loci homologous to a single probe were suffixed with designations *A*, *B*, etc. Clones of several known genes were also used in the comparative mapping study: small subunit ribulose bisphosphate carboxylase (*Rbcs*), chlorophyll *a/b* binding protein (*Cab*), and the 45s major ribosomal repeat (*R45s*). The Rbcs and Cab clones were from tomato (PICHERSKY *et al.* 1985, 1986) and the ribosomal clone was from pea (JORGENSEN *et al.* 1982). The clones used in this study had previously been mapped to orthologous loci in tomato, and are distributed throughout 94% of the 1237 cM tomato RFLP map at intervals averaging 11 cM (TANKSLEY *et al.* 1987; Figure 1B).

Whole plasmids were either nick-translated or random-hexamer-labeled with ^{32}P-dCTP (RIGBY *et al.* 1977, FEINBERG and VOGELSTEIN 1983). Potato parental survey or progeny filters were hybridized overnight as previously described (BERNATZKY and TANKSLEY 1986b). Filters were washed to medium stringency (0.5 × SSC, 65°) and placed on X-ray film for 1–5 days.

Data from eleven isozyme markers and *Y*, a morphological marker determining tuber flesh color (HOWARD 1970), segregating in the same diploid population, were kindly supplied by DAVE DOUCHES. These data were included in the mapping analysis by their co-segregation with the DNA markers.

RFLP analysis and map construction: Enzyme-probe combinations were selected for which the *tbr-chc* parent appeared to be heterozygous, while the other parent (*phu*) was either homozygous, or heterozygous but with different alleles. Potential heterozygosity with a given probe was inferred by the presence of more than one hybridizing restriction fragment per digestion on parental survey filters, and polymorphism between the parents required that at least one fragment be unique to the parent in question. Segregation of alleles from *tbr-chc* were verified and scored in the progeny. Analysis of segregation data was performed on an IBM PC/AT computer using SPSS software. Recombination frequencies were converted to map units according to KOSAMBI (1944).

In some instances, heterozygous loci in the *phu* parent were also observed to segregate in the progeny, and a second set of mapping data was collected.

RESULTS

Description of the potato linkage map: A total of 134 segregating DNA and isozyme markers were assigned to 12 linkage groups in the potato genome. The high degree of conservation of chromosome content between tomato and potato (see following section) allowed the assignment of the potato linkage groups to chromosomes *1* through *12* by homeology to the tomato chromosomes (Figure 1A). Each of the chromosomes is marked by from 7 to 18 linked loci, with adjacent markers separated by 0–30 map units.

The linkage group *Idh1-Skdh1*, which DOUCHES and QUIROS (1987) reported to span a centromeric region of an unidentified potato chromosome, cosegregated in potato with several DNA markers from tomato chromosome *1*, placing it in the same map position in the two species. Linkage analysis also places six other isozyme loci—*Prx2*, *Pgm1*, *Pgm2*, *Got2* and *Pgi1*—in chromosomal locations corresponding with those previously reported for tomato. Three isozyme loci—*6Pgdh3*, *Dia1* and *Mdh3*—which have not yet been mapped in tomato were found to be tightly linked with RFLP markers on chromosomes *5* and *7* in potato. The chromosome *5* isozyme markers (*6Pgdh3* and *Dia1*) have been reported to span a centromeric region in potato (DOUCHES and QUIROS 1988), and one of them, *6Pgdh3* had previously been assigned to chromosome *5* in tomato by trisomic dosage analysis but not mapped to a specific position within the chromosome (TANKSLEY and KUEHN 1985).

Alleles of *Pgi1*, *Mdh3* and *Y* were segregating only from the *phu* parent, and the inclusion of these three loci in the potato map was made possible by their linkage with RFLP markers for which both parents were heterozygous. The markers mapped by segregation from *phu* are designated in Figure 1A with an asterisk.

Two markers, tomato genomic clone *TG218* and a third locus for CD21 (*CD21C*), which were not polymorphic in tomato were mapped in potato to chromosomes *7* and *8*, respectively. The locus *CD21C* extends potato chromosome *8* beyond the terminal DNA marker (*CD29*) on the tomato homeolog (Figure 1, A and B).

Comparison of the tomato and potato linkage maps: The tomato map, with which the potato map is being compared, was based on an F_2 population from

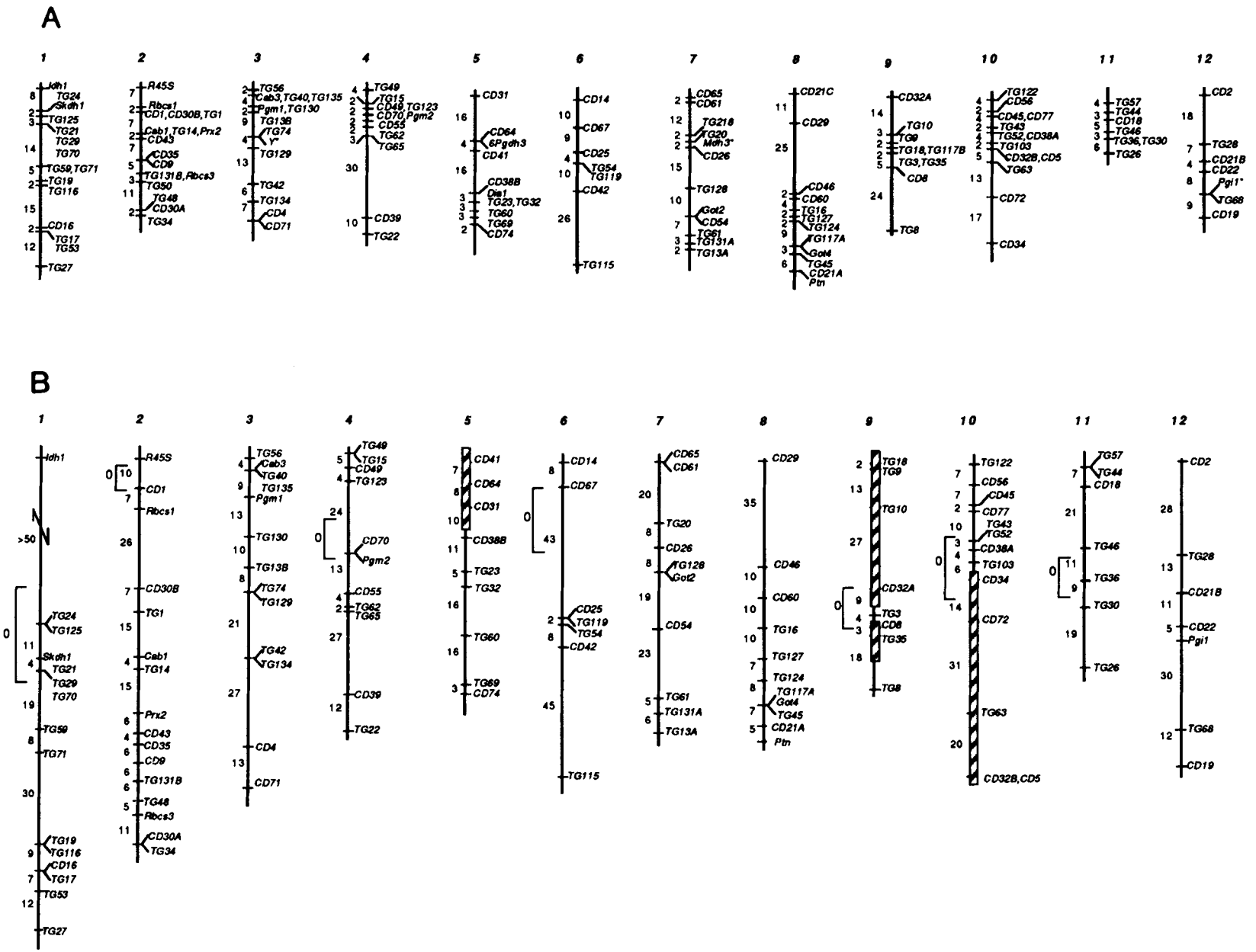

FIGURE 1—Comparative genetic maps of potato and tomato based on a common set of DNA clones. Two point linkage distances between adjacent markers are based on KOSAMBI (1944) map units. A, Potato: Asterisks indicate markers mapped by segregation of alleles from *S.phu.* B, Tomato: Hatched boxes represent intervals in which the order of markers is inverted between the two genomes. Brackets indicate approximate position of centromeres.

a cross between inbred accessions of *L. esculentum* and *L. pennellii* (BERNATZKY and TANKSLEY 1986b, TANKSLEY *et al.* 1987). On the tomato map, the loci we have examined in potato span a total of 1189 cM, and are distributed throughout 94% of the tomato genome (Figure 1B).

Of the tomato cDNA and genomic clones examined, all but two hybridized to potato genomic DNA under conditions of medium stringency (0.5 × SSC, 65°). Thus, for nearly every tomato genomic sequence or cDNA tested it was possible to find a homologous counterpart in potato.

In addition to the homology of DNA sequences throughout the tomato and potato genomes, the linkage order of those sequences on the chromosomes is remarkably well conserved. A comparison of the arrangement of loci in tomato and potato reveals that all DNA sequences mapped in potato can be assigned to linkage groups corresponding to chromosomes *1–12* in tomato (Figure 1, A and B). Nine chromosomes (*1, 2, 3, 4, 6, 7, 8, 11* and *12*) appear to have been unaltered by any detectable rearrangements. Any rearrangements that may have occurred within the intervals between two adjacent markers examined would have gone undetected in our analysis; however, on the average, the markers were linked at fairly close intervals (*ca.* 11 cM).

Evolution by paracentric inversions: Three of the tomato/potato homeologs differ by what appear to be paracentric inversions (Figure 1, A and B). One end of each of the inversions detected coincides with the approximate position of the centromere in the tomato homeolog. On chromosomes *5* and *10*, terminal regions, encompassing approximately 20 cM and 68 cM, respectively, on the tomato map, were found to be inverted between the tomato and potato genomes. The inversion on chromosome *5* is marked by three loci, *CD31*, *CD67* and *CD41*, and that on chromosome *10* by five, *CD34, CD72, CD63, CD5* and *CD32B*. Both arms of chromosome *9* have sustained paracentric inversions—one interstitial and the other terminal.

The average length of the four putative inversions differentiating the potato and tomato genomes is 34 cM (based on the tomato map), and together these segments constitute 11% of the genome.

Reduced recombination in potato *vs.* tomato chromosomes: The orthologous loci mapped in tomato cover 1189 cM in tomato, whereas the same markers in potato define only 606 cM. A paired *T*-test using sets of intervals revealed that the reduced recombination in potato chromosomes compared with tomato is significant ($P < 0.001$). The reduction in recombination appears to have affected all chromosomes since each of the potato chromosomes has a reduced genetic length (1.4–3.6-fold shorter) compared with the corresponding tomato chromosome. The mean interval

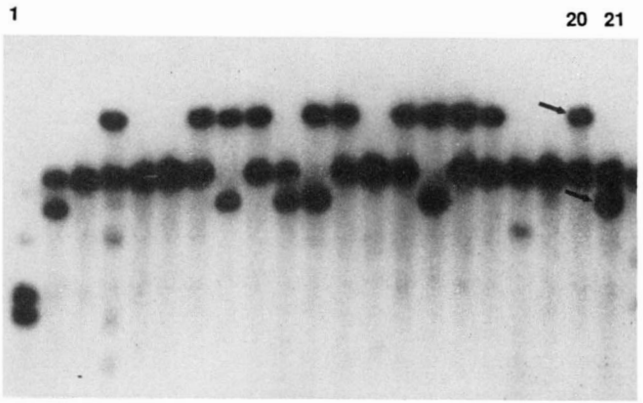

FIGURE 2.—Autoradiogram from hybridization of Southern blot of genomic DNA from segregating potato progeny (*Dra*I digest) with *TG65*. Lane 1, tomato; lanes 2–19, potato progeny; lane 20, T704 (*S.tbr-S.chc*); lane 21, 84S10 (*S.phu*). Arrows indicate restriction fragments unique to each parent.

length between adjacent markers in potato was 50% less than that found in tomato. However, in some regions of the potato chromosomes, recombination was even more severely reduced. For example, certain regions on chromosomes *1, 2, 3, 4, 5, 8* and *12* showed recombination in potato less than 25% of that observed in tomato. The proximal region on the long arm of chromosome *2* (between *CD1* and *CD43*) is an especially striking example since the interval contains 79 cM in tomato, but only 9 cM in potato.

The potato population was segregating for loci heterozygous in the *tbr-chc* parent and in some instances, also for loci heterozygous in the *phu* parent (Figure 2). As an independent assessment of recombination in the Solanum genome, linkage analysis was conducted for 12 randomly selected intervals bounded by markers segregating from the *phu* parent. These data, while not representing all loci, provided a basis for comparing recombination frequency among tomato, the interspecific potato parent, and the *phu* clone (Table 1). Of the intervals compared, only one varied significantly among the three populations. On chromosome *1*, the interval between *TG125* and *TG19* showed reduced recombination in the *tbr-chc* parent as compared with tomato—21 *vs.* >50 cM. However the rate of recombination in the *phu* parent for this interval (49 cM) was similar to that found in tomato.

Aberrant segregation ratios: Significant deviations from the expected 1:1 ratio were found at 28% of the loci segregating in the *tbr-chc* parent. The loci showing deviant ratios cluster on parts of chromosomes *1, 6, 7, 8* and *10* (Table 2, Figure 3). These regions were also among those found to exhibit reduced recombination relative to tomato.

The majority of the segregating loci (28/31 = 90%) scored from the *phu* parent fit the expected 1:1 ratio. Two of the three loci showing skewed segregation from this parent are tightly linked on chromosome *4*.

Restriction fragment length polymorphism: With

TABLE 1

Comparison of recombination fraction in selected intervals among three mapping populations; tomato (*L. esc* × *L. pen* F_2), potato P1 = T704 (*S. tbr* × *S. chc*), and potato P2 = 84S10 (*S. phu*)

		Recombination fraction		
			Potato	
Interval	Chromosome	Tomato	P1	P2
TG19–TG53	*1*	0.14	0.20	0.23
TG19–TG125	*1*	0.50	0.21*	0.49
TG42–TG74	*3*	0.22	0.16	0.07
CD55–TG62	*4*	0.05	0.02	0.10
TG62–TG65	*4*	0.03	0.03	0.06
CD39–TG22	*4*	0.12	0.10	0.08
CD31–CD41	*5*	0.18	0.16	0.10
TG218–TG20	*7*	No data[a]	0.02	0.02
TG20–CD26	*7*	0.08	0.02	0.02
TG16–TG127	*8*	0.09	0.02	0.00
TG127–TG117	*8*	0.18	0.16	0.10
TG68–TG19	*12*	0.12	0.09	0.09

* $P < 0.05$.

[a] TG218 was not mapped (not polymorphic) in tomato.

TABLE 2

Loci in the potato genome with monogenic ratios deviating from the expected (1:1) Mendelian ratio ($P \leq 0.05$)

Chromosome	Locus	Ratio
1	*TG125*	41:24
1	*TG71*	38:22
1	*TG19*	38:20
1	*Skdh1*	40:23
2	*CD43*	21:37
2	*CD35*	24:41
2	*TG34*	18:35
3	*TG129*	37:21
6	*CD14*	56:7
6	*CD67*	43:10
6	*TG25*	47:15
6	*CD25*	44:21
6	*TG54*	36:13
6	*TG119*	41:17
6	*CD42*	42:20
7	*TG20*	40:19
7	*TG128*	45:21
7	*CD54*	45:18
7	*TG61*	47:14
7	*TG13A*	43:13
8	*TG127*	23:43
8	*TG124*	22:44
8	*TG117A*	16:50
8	*Got4*	15:49
8	*TG45*	16:49
8	*CD21A*	16:50
8	*Ptn*	16:50
10	*TG122*	19:37
10	*CD56*	24:41
10	*CD77*	24:42
10	*TG43*	24:31
10	*TG63*	22:39

one or more of the 11 restriction enzymes used in this study, potential polymorphic heterozygosity was found in the *tbr-chc* parent for 98% of the DNA clones examined, compared with 81% for the *phu* parent. The level of heterozygosity observed in the *phu* parent suggests that natural populations of this outcrossing species of Solanum are likely to maintain significant amount of restriction fragment length polymorphism. Restriction enzymes most successful in detecting polymorphism between the parents were *Eco*RI, *Eco*RV, *Hin*dIII, *Dra*I and *Xba*I.

Comparison of cDNA and genomic clones: cDNA clones and single copy genomic clones were nearly equal in the frequency with which they detected restriction fragment length polymorphism in the two potato parents. With all of the enzyme-probe combinations used, the cDNAs and the genomic clones detected polymorphism in 166/324 = 51%, and 342/572 = 60% of the cases, respectively.

Changes in genomic clone copy number and homology: In contrast to cDNA clones, two of the tomato single copy genomic clones were found to hybridize with multiple copies in the potato genome: clones *TG37* and *TG12*, which mark single loci on chromosomes *4* and *10* in tomato, each hybridized to repetitive elements and could not be mapped in potato (Figure 4A).

Two additional single copy genomic clones, *TG5* and *TG51* from tomato chromosomes *7* and *1*, could not be mapped in potato due to lack of sufficient homology with corresponding potato sequences (Figure 4B).

DISCUSSION

Chromosome evolution: Our knowledge about chromosome evolution in higher plants is based largely on meiotic analysis and comparisons of karyotypes. The former is necessarily restricted to interfertile species, as the analysis is performed on hybrid plants. The latter, while not limited to crossable species, has poor resolution, since changes in karyotypes can be brought about by many different processes and often these changes are not distinguishable by morphological comparisons of mitotic chromosomes.

The family Solanaceae is interesting in that it contains a highly diverse group of species, yet most share the same basic chromosome number ($x = 12$). Changes in basic chromosome number, especially dysploid decreases, are believed to be facilitated by chromosomal translocations (BROWN 1972). We report here that, since the divergence of potato and tomato from their last common ancestor, the only detectable chromosomal changes have been paracentric inversions. The occurrence of only this type of rearrangement, which does not result in changes in karyotype, is consistent with cytological observations reporting the conservation of relative chromosomal arm lengths between the two species (YEH and PELOQUIN 1965).

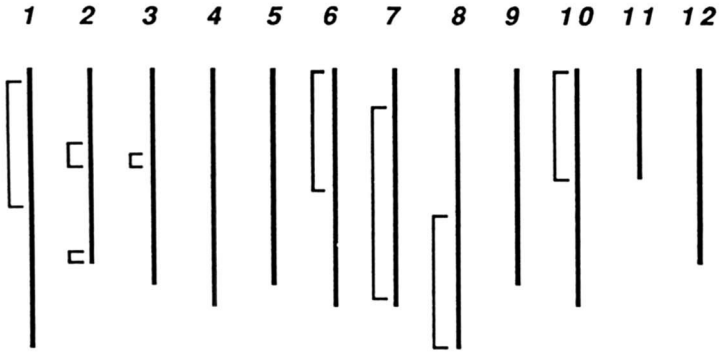

FIGURE 3.—Regions of the potato genome exhibiting aberant monogenic ratios ($P < 0.05$).

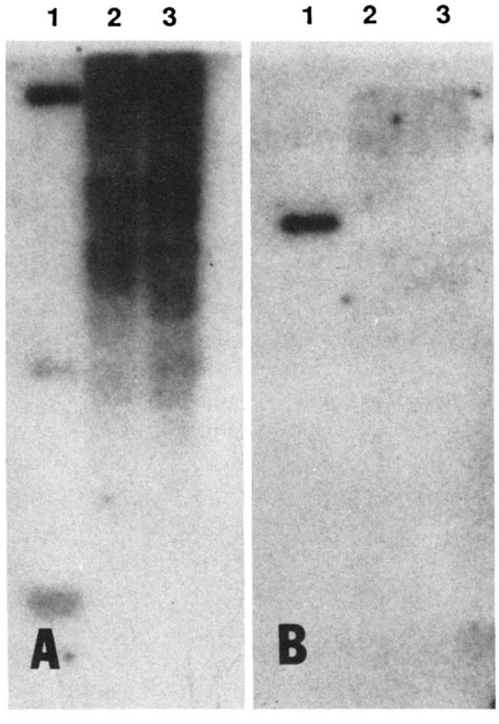

FIGURE 4.—Autoradiograms from hybridization of Southern blots of tomato and potato genomic DNA (*Eco*RV digests) with tomato clones. Lane 1, tomato; lane 2, potato $2n = 2x = 24$; lane 3, potato $2n = 2x = 48$. A, Clone *TG12* present in single copy in tomato and multiple copy in potato. B, Clone *TG5*: single copy in tomato and not homologous in potato.

The lack of translocations and pericentric inversions may be due to a selective disadvantage of these types of chromosomal rearrangement compared with paracentric inversions. A well-documented precedent for the predominance of paracentric over pericentric inversions is the phylogenetic work with Drosophila species (STONE 1955; STONE, GUEST and WILSON 1960; CARSON 1970). An observation explaining the survival of paracentrics in Drosophila has been proposed to exist in angiosperms as well (BROWN 1972; C. M. RICK, personal communication). By this mechanism, the specific orientation of cells in the linear tetrad of micro- or macrospores ensures that duplication- and deficiency-nuclei resulting from crossing over in the loop of inversion heterozygotes are not included in the gametes. Cytological evidence for paracentric inversions from bridges and fragments has been reported for several plant species (RICHARDSON 1936), but in the past, the resolution of chromosome mapping has not been fine enough to rule out the presence of pericentrics. Whatever the reasons for the predominance of paracentric inversions in the evolution of the tomato and potato, the predicted outcome has been the maintenance of chromosome number and arm ratio simultaneous with the reshuffling of gene order within chromosome arms.

Chromosome translocations are not a forbidden mutation in solanaceous species, since translocations can be induced and stably maintained in tomato (GILL *et al.* 1980) and are naturally occurring in the genus Capsicum (garden pepper) (PICKERSGILL, HEISER and MCNEILL 1978; TANKSLEY 1984). Comparative mapping of tomato and pepper chromosomes using RFLP markers has revealed significant linkage group rearrangement, some of which must have involved chromosomal translocations (TANKSLEY *et al.* 1988). Pepper ($2n = 2x = 24$), unlike potato, differs significantly from tomato in its genome size (C = 2.76, *vs.* C = 0.74 in tomato). It is not surprising that the fourfold change in DNA content which has occurred since the divergence of tomato and pepper was accompanied by a larger amount of genome rearrangement than is seen between tomato and potato.

In generalizing about the comparative chromosome arrangement of the two species examined in this study, one must proceed cautiously in light of the fact that polymorphism for variant chromosome structure may exist within as well as between populations of different species. Although in Drosophila the extent of chromosomal rearrangement within and among species does not necessarily parallel morphological diversity or taxonomical groupings (BOCK 1971; DOBZHANSKY 1972), it is clear that structural differences do play a fundamental role in the differentiation of species. Surveys of chromosomal polymorphism among species of Lycopersicon and Solanum could be accomplished by comparative genetic mapping, and would contribute to our understanding of the importance of this type of mutation in the evolution of fertility barriers in this important plant family.

Recombination: The segregation data used to generate the tomato and potato maps presented here were derived from single segregating populations. Since meiotic recombination can vary among individuals within a species, it would be premature to conclude that potato chromosomes, in general, experience less crossing over than do their tomato counterparts. An additional confounding factor is that in both tomato and potato, interspecific crosses were used to determine map distances, and this is known to affect recombination (RICK 1969).

The outcome of our comparison of recombination in the *tbr-chc* versus the *phu* potato parents (Table 1) suggests that, at least in one instance, the lesser recombination seen in *tbr-chc* as compared to tomato is not a general phenomenon in potato, but was a function of the cross used for determining recombination.

DOUCHES and QUIROS (1987, 1988) also noted reduced recombination levels for several chromosome regions when they compared gene-centromere map distances in the interspecific hybrid used in this study (*tbr-chc*, T704) with those of "nonhybrid" diploid stocks of *S. tuberosum*. The *tbr-chc* parent is homozygous for the parallel spindles mutation (*ps*) which affords it the option of producing 2*n* gametes by first division restitution (FDR) (MOK and PELOQUIN 1975); but it does not express any of the recognized asynaptic or desynaptic mutant genes (reviewed in DOUCHES and QUIROS 1988) which have been shown to reduce recombination in other diploid Solanum stocks.

Although the hypothesis is difficult to test, it would be interesting to determine if areas of the potato genome that we and others (DOUCHES and QUIROS 1988) have identified as having extremely reduced recombination in interspecific populations might be indicative of structural polymorphism among *Solanum* species. If the interspecific potato parent used to construct the present map were heterozygous for inversions, one consequence would be genotype-specific (*tbr-chc* vs. *phu*) reduced recombination in distinct regions of the genome such as we have observed on chromosome *1* (see Table 1). The reduced recombination we observed between the genetic maps of tomato and potato could be due to the presence of unrecognized genes which influence crossing over or to a lack of homosequentiality of the genomes on which the potato map was based.

Nucleotide sequence homology of potato and tomato DNA: It is apparent from this study and from the work of ZAMIR and TANKSLEY (1988) that there is a high degree of conservation of most coding regions and single copy DNA sequences between tomato and potato, and that the linkage groups of the two species are well-conserved. In contrast, most highly repeated fraction of the two genomes has diverged to the point that there is little or no cross-hybridization. Only one of the three most highly repeated, non-ribosomal DNA repeats from tomato is found in potato (GANAL, LAPITAN and TANKSLEY 1988; SCHWEIZER *et al.* 1988). Some of the more highly repetitive, fast-evolving sequences are tandemly organized and might be expected to undergo rapid and concerted changes within isolated species (ARNHEIM 1983). However, others are highly interspersed throughout the genome (GANAL, LAPITAN and TANKSLEY 1988). It is apparent from this report that these interspersed sequences must also be evolving in a concerted manner, independently of gross chromosomal rearrangements.

Uniting potato and tomato genetics: Potato and tomato, being major crop species, have long histories of genetic and breeding research. Despite the fact that they are members of closely related genera, there has been little common ground between the two disciplines. Genetic maps based on a common set of DNA probes provide a basis for beginning to unite the two fields. Based on the comparative maps reported here, we now know which regions of the potato and tomato chromosomes are conserved, and where the differences occur. In tomato, more than 400 molecular markers have now been located on the genetic map (TANKSLEY *et al.* 1987; and unpublished data, this laboratory). Based on the position of the clones already mapped in potato, it is possible to predict the position of the additional 200 cloned markers from tomato. For practical purposes then, the potato map is comprised of the same number of loci mapped in tomato. Positions of unmapped isozyme loci in potato can also be predicted based on their position in the tomato map. The potato and tomato comparative maps have already provided a basis for determining the chromosomal localization of patatin-coding genes in both species (S. D. TANKSLEY, M. W. BONIERBALE and W. D. PARK, unpublished data).

Perhaps one of the most exciting outcomes of maps based on common clones will be the ability to ask questions about the homology and orthology of genes that have not yet been cloned and whose gene products are not known. For example, tomato and potato are common hosts to pathogens from a wide range of classes—including nematodes, viruses, bacteria and fungi (HOOKER 1981). Resistances to many shared pests have been identified among the genetic resources of both species, yet the relationship among resistance genes from the two species is unknown. Common map positions may be used to infer homology of resistance genes found in these two, heretofore, independent pools of resources, and theories concerning the inheritance and mechanisms of gene action proposed for one species may be suggested for the other.

Practical aspects of potato RFLP mapping: Prac-

tical applications of the reported linkage map to potato genetics and breeding will stem from the association of molecular markers with useful genes. The genetic resources of the potato are vast, and many sources of desirable traits have been identified in wild species (HANNEMAN and BAMBERG 1986), yet these resources have seldom been included in acceptable cultivars. Among the barriers which can impede the exploitation of wild species by conventional breeding methods are (1) the association of desired traits with unfavorable agronomic traits from unadapted sources, and (2) the complicated nature of the inheritance of certain desirable traits.

Genes controlling quantitatively inherited characters in tomato (OSBORN, ALEXANDER and FOBES 1987; TANKSLEY and HEWITT 1988), pepper (TANKSLEY and IGLESIAS-OLIVAS 1984), and maize (STUBER, EDWARDS and WENDEL 1987; EDWARDS, STUBER and WENDEL 1987) have been detected with molecular markers. The ability to detect, map, and monitor loci affecting both qualitative and quantitative traits by their linkage to molecular markers promises to increase the efficiency of their introgression into desirable genetic backgrounds. The mapping of genes of interest based on their linkage with RFLP markers may enhance selection in segregating populations by permitting a more exacting assessment of the genotype of individuals than is possible based on phenotype or progeny testing alone. Marker-enhanced selection may also be used to identify recombinant individuals which bear the genes to be introgressed with minimal amounts of flanking DNA (YOUNG and TANKSLEY 1988).

The fact that chromosome contents are conserved between potato and tomato suggests the possibility of producing chromosome substitution lines between the species. Reports have already been issued regarding somatic fusion of the two species (MELCHERS, SACRISTAN and HOLDER 1978). Chromosome substitution lines might be used as an intermediate step in the introgression of genes between the potato and tomato gene pools. Long stretches of homosequential chromosome segments could facilitate homologous recombination in meiosis of future chromosomal exchange lines that might be derived from somatic fusion products.

The heterozygous, polyploid constitution of the cultivated potato is probably the principal reason for the previous lack of a genetic linkage map. Although the current map was developed at the diploid level, the linear order of the loci detected is expected to be the same at the tetraploid level, and the map reported in this paper should therefore serve most genetic and breeding studies in the cultivated potato. A quality of RFLPs of particular importance to breeders of polyploid, cross-pollinating crops is their codominant nature. RFLPs will be a valuable tool for assessing allelic frequencies in individuals and monitoring genotypic shifts in populations. The selection of breeding parents with high plex levels for particular desirable alleles can be accomplished directly, and the ability of alternate breeding schemes to approach the goals of particular population improvement programs can be efficiently evaluated.

Thanks to MARTIN GANAL, MARION ROEDER and JIM PRINCE for reviewing the manuscript, and to STEFFIE DAVID for typing. This work was supported by National Science Foundation grant DCB-8517773 to S. D. T. and by a contract between Cornell University and the International Potato Center.

LITERATURE CITED

ARNHEIM, N., 1983 Concerted evolution in multigene families. pp. 38–61. In: *Evolution of genes and proteins*, Edited by R. KOEHN and M. NEI. Sinauer, Sunderland, Mass.

BERNATZKY, R., and S. D. TANKSLEY, 1986a Majority of random cDNA clones correspond to single loci in the tomato genome. Mol. Gen. Genet. **203:** 8–14.

BERNATZKY, R., and S. D. TANKSLEY, 1986b Toward a saturated linkage map in tomato based on isozymes and random cDNA sequences. Genetics **112:** 887–898.

BOCK, I. R., 1971 Intra- and interspecific chromosomal inversions in the *Drosophila bipectinata* species complex. Chromosoma **34:** 206–229.

BROWN, W. V., 1972 *Textbook of Cytogenetics.* C. V. Mosby, St. Louis.

CARSON, H. L., 1970 Chromosome tracers of the origin of species. Science **168:** 1414–1418.

D'ARCY, W. G., 1976 The classification of the Solanaceae. pp. 3–47. In: *The Biology and Taxonomy of the Solanaceae*, Edited by J. G. HAWKES, R. N. LESTER and A. D. SKELDING. Academic Press, London.

DOBZHANSKY, T., 1972 Species of Drosophila—new excitement in an old field. Science **177:** 664–669.

DOUCHES, D. S., and C. F. QUIROS, 1987 Use of 4X-2X crosses to determine gene-centromere map distances of isozyme loci in Solanum species. Genome **29:** 519–527.

DOUCHES, D. S., and C. F. QUIROS, 1988 Genetic recombination in a diploid synaptic mutant and a *Solanum tuberosum* × *S. chacoense* diploid hybrid. Heredity **60:** 183–191.

EDWARDS, M. D., C. W. STUBER and J. F. WENDEL, 1987 Molecular-marker-facilitated investigations of quantitative-trait loci in maize. I. Numbers, genomic distribution and types of gene action. Genetics **1156:** 113–125.

FEINBERG, A. P., and B. VOLGELSTEIN, 1983 A technique for radiolabeling DNA restriction fragments to a high specific activity. Anal. Biochem. **132:** 6–13.

GANAL, M. W., N. L. V. LAPITAN and S. D. TANKSLEY, 1988 A molecular and cytogenetic survey of major repeated DNA sequences in tomato (*Lycopersicon esculentum*). Mol. Gen. Genet. **213:** 262–268.

GILL, B. S., C. R. BURNHAM, G. R. STRINGHAM, J. T. STOUT and W. H. WEINHEIMER, 1980 Cytogenetic analysis of chromosomal translocations in the tomato: preferential breakage in heterochromatin. Can. J. Genet. Cytol. **22:** 333–341.

HANNEMAN, R. E., JR., and J. B. BAMBERG, 1986 Inventory of tuber-bearing Solanum species. Wisc. Agric. Res. Stn. Bull. 533.

HOOKER, W. J. (Editor), 1981 *Compendium of Potato Diseases.* American Phytopatholog. Society, St. Paul, Minn.

HOWARD, H. W., 1970 *Genetics of the Potato.* Springer-Verlag, New York.

HUAMAN, Z., and R. W. ROSS, 1985 Updated listing of potato

species names, abbreviations and taxonomic status. Am. Potato J. **62:** 629–641.

JORGENSEN, R. A., R. E. CUELLAR and W. F. THOMPSON, 1982 Modes and tempos in the evolution of ribosomal RNA genes in legumes. Carnegie Inst. Year Book **81:** 98–101.

KOSAMBI, D. D., 1944 The estimation of map distances from recombination values. Ann. Eugen. **12:** 172–175.

MELCHERS, G., M. D. SACRISTAN and A. A. HOLDER, 1978 Somatic hybrid plants of potato and tomato regenerated from fused protoplasts. Carlsburg Res. Commun. **43:** 203–218.

MOK, D. W. S., and S. J. PELOQUIN, 1975 Three mechanisms of 2*n* pollen formation in diploid potatoes. Can. J. Genet. Cytol. **17:** 217–225.

OSBORNE, T. C., D. C. ALEXANDER and J. F. FOBES, 1987 Identification of restriction fragment length polymorphisms linked to genes controlling soluble solids content in tomato fruit. Theor. Appl. Genet. **73:** 350–356.

PICHERSKY, E., R. BERNATZKY, S. D. TANKSLEY, R. B. BREIDENBACH, R. B. KAUSCH and A. P. CASHMORE, 1985 Molecular characterization and genetic mapping of two clusters of genes encoding clorophyll a/b-binding proteins in *Lycopersicon esculentum.* Gene **40:** 247–258.

PICHERSKY, E., R. BERNATZKY, S. D. TANKSLEY and A. R. CASHMORE, 1986 Evidence for selection as a mechanism in the concerted evolution of *Lycopersicon esculentum* (tomato) genes encoding the small subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase. Proc. Natl. Acad. Sci. USA **83:** 3880–3884.

PICKERSGILL, B., C. B. HEISER and J. MCNEILL, 1978 Numerical taxonomic studies on variation and domestication in some species of *Capsicum.* pp. 679–700. In: *The Biology and Taxonomy of the Solanaceae,* Edited by J. G. HAWKES, R. N. LESTER and A. D. SKELDING. Academic Press, London.

RICHARDSON, M. M., 1936 Structural hybridity in *Lilium martagon album* × L. HANSONII. J. Genet. **32:** 411–449.

RICK, C. M., 1969 Controlled introgression of chromosomes of Solanum pennellii into *Lycopersicon esculentum*: segregation and recombination. Genetics **62:** 753–768.

RIGBY, P., M. DIECKMAN, C. RHOADES and P. BERG, 1977 Labeling deoxyribonucleic acid to high specific activity in vitro by nick-translation with DNA polymerase I. Nucleic Acids Res. **7:** 1263–1281.

SCHWEIZER, G., M. GANAL, H. NINNEMAN and V. HEMLEBEN, 1988 Species-specific DNA sequences for identification of somatic hybrids between *Lycopersicon esculentum* and *Solanum acaule.* Theor. Appl. Gen. **75:** 679–684.

STONE, W. S., 1955 Genetic and chromosomal varibility in Drosophila. Cold Spring Harbor Symp. Quant. Biol. **20:** 256–270.

STONE, W. S., W. GUEST and F. D. WILSON, 1960 The evolutionary implications of the cytological polymorphism and phylogeny of the *virilis* group of *Drosophila.* Proc. Nat. Acad. Sci. USA **46:** 350–361.

STUBER, C. W., M. D. EDWARDS and J. F. WENDEL, 1987 Molecular-marker-facilitated investigations of quantitative-trait loci in maize. II. Factors influencing yield and its component traits. Crop Sci. **27:** 639–648.

TANKSLEY, S. D., 1984 Linkage relationships and chromosomal locations of enzyme-coding genes in pepper, *Capsicum annuum.* Choromosoma **89:** 352–360.

TANKSLEY, S. D., AND J. HEWITT, 1988 Use of molecular markers in breeding for soluble solids content in tomato- a reexamiantion. Theor. Appl. Genet. **75:** 811–823.

TANKSLEY, S. D., and G. D. KUEHN, 1985 Genetics, subcellular localization, and characterization of 6-phosphogluconate dehydrogenase isozymes in tomato. Biochem. Genet. **23:** 441–454.

TANKSLEY, S. D., and J. IGLESIAS-OLIVAS, 1984 Inheritance and transfer of multiple-flower character from Capsicum chinense into *Capsicum annuum.* Euphytica **33:** 769–777.

TANKSLEY, S. D., M. A. MUTSCHLER and C. M. RICK, 1987 Linkage map of the tomato (*Lycopersicon esculentum*) (2*n* = 24). pp. 655–669. In: *Genetic Maps 1987 A Compilation of Linkage and Restriction Maps of Genetically Studied Organisms,* Edited by S. J. O'BRIEN. Cold Spring Harbor Laboratory, Cold Spring Harbor, N.Y.

TANKSLEY, S. D., J. MILLER, A. PATERSON and R. BERNATZKY, 1987 Molecular mapping of plant chromosomes. (SDT JM AP RB 1987 Molecular mapping of plant chromosomes.) pp. 157–173. In: *Chromosome Structure and Function,* Edited by J. P. GUSTAFSON and R. APPELS. Plenum Press, N.Y.

TANKSLEY, S. D., R. BERNATZKY, N. L. LAPITAN and J. P. PRINCE, 1988 Conservation of gene repertoire but not gene order in pepper and tomato. Proc. Natl. Acad. Sci. USA **85:** 6419–6423.

YEH, B. P., and S. J. PELOQUIN, 1965. Pachytene chromosomes of the potato (*Solanum tuberosum*, group *andigena*). Am. J. Bot. **52:** 1014–1020.

YOUNG, N. D., and S. D. TANKSLEY, 1988 Restriction fragment length polymorphism analysis of tomato lines generated by introgression of the *Tm-2* and *Tm-2a* virus resistance genes from *L. peruvianum.* (in press)

ZAMIR, D., and S. D. TANKSLEY, 1988 Tomato genome is compromised largely of fast-evolving, low copy-number sequences. Mol. Gen. Genet. **213:** 254–261.

Communicating editor: B. BURR